## COLIAS CROCEUS GEOFFROY IN FOURCROY (LEPIDOPTERA: PIERIDAE) IN ARGYLLSHIRE, AND SOME SUGGESTIONS ON A FOR FURTHER STUDY

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I collected a male and female of *C. croceus* from the disused quarry at Oban, Argyllshire (56° 25′ 06″ N, 5° 26′ 49″ W), 5.viii.1992, and a further female from the ruins of the Oban 'Hydro', 8.viii.1992; I took a further eight males and six females from North Shian, Argyllshire (56° 32′ 32″ N, 5° 24′ 03″ W), 14.viii.1992. *C. croceus* is a rare migrant in Scotland, with just 22 recorded migrations into the country, the most recent of these in 1976 (Thomson, 1980; Gardiner, 1984). There appear to be no records however for Oban or North Shian. The quarry, 20–50 m altitude, was sparsely vegetated, in contrast to the 'Hydro' site 0.6 km to the WSW; the 'Hydro' and North Shian habitats comprised open areas at 60 m and 10–30 m altitude respectively, well vegetated with various Gramineae, *Lotus* and *Trifolium*, on southfacing mixed woodland slopes. All specimens were of the typical orange form and were taken between 12.00 and 14.00 h BST.

Insects arriving in Scotland in June occasionally produce a native Scottish brood in August (Thomson, 1980). I believe that *C. croceus* was reported on the Isle of Mull in June 1992 (Martin C. White, citing Neil Cravenscroft, pers. comm.), suggesting that the specimens listed above represent such a brood. Whether these specimens originate locally or from Mull however is not ascertained. On account of the scarcity of the species in Scotland, I attempted to pair the animals in order to obtain a further generation of the Scottish stock and to test for the possible presence of the *helice* gene in the parental sample. Although the species does not normally survive British winters (Thomas & Lewington, 1991), the species can overwinter as a larva under mild and dry conditions (Eveleigh, 1984). Below I present some findings from the breeding programme and suggest some avenues of further research.

The North Shian specimens were transported to Oban in  $2\frac{1}{2}$ " diameter perspexbottomed card boxes. The butterflies were placed outdoors over cut *L. corniculatus L.* in an improvised breeding cage constructed from a net bag, an earthenware pot and lengths of cane. Food and water were provided by cotton wool pads charged with 10% honey solution. These were placed on top of the netting and replaced 2–3 times daily, when the cage was sprayed liberally with water. This protocol was continued, and from 16.viii.1992 in Colwyn Bay, Clwyd, until my return to Reading on 23.viii.1992 when the insects were transferred to a cage containing growing *L. corniculatus* but otherwise similarly maintained. Ova laid on the cut foodplant were placed indoors still attached to the leaves. On hatching, the larvae were transferred to the growing plant.

On 1.x.1992 I counted 132 larvae, 30 of which I dispersed elsewhere. Twenty adults eclosed over the period 17.x.1992 to 23.xi.1992 (cohort 1). Temperature (mean  $\pm$  SD) over the period 23.viii.1992 to 23.xi.1992 was  $10.8 \pm 5.4^{\circ}$ C. At the beginning of December the remaining larvae were placed indoors in 5" diameter translucent perspex tubs, under natural daylength but away from direct moisture, and these replenished with cut foodplant at three-day intervals. Twenty-three of these animals survived and eclosed over the period 20.xii.1992 to 15.i.1993 (cohort 2). Temperature over the period 24.xi.1992 to 30.xi.1992 was 7.8  $\pm$  4.1°C. Outdoor temperature over the remainder of

the rearing period was  $4.6 \pm 4.9^{\circ}$ C; although indoor temperature was not recorded during this period, it might be expected to be warmer. The above results represent an overall survival ratio of 38%.

The  $F_1$  yielded ten typical and twelve white f. *helice* females, indicating the presence of the *helice* gene among the parental males; the allele is dominant but sexlimited in its expression (Ford, 1945). Hence, if one parent of a two-parent brood carries the *helice* gene, 50% of female offspring will be f. *helice*. While the 50% type to 50% f. *helice* ratio obtained might therefore suggest that all the male parents carried the gene, this is unlikely, so it can be concluded only that at least one of the male parents carried the gene and that variable  $F_1$  survival from the various parent females produced, by chance, an equal type to f. *helice* ratio.

The emergence of cohort 2 over December and January indicates that the brood had to a degree been 'forced', suggesting that higher temperatures than normal for the winter were acting on the larvae. In many Lepidoptera, larvae grow more quickly at warmer temperatures but weigh less at maturity (Ray, 1960), and indeed the adults of cohort 2 were noticeably smaller than those of cohort 1 supporting the above contention. In both sexes, the orange ground colour was paler in cohort 2 than in cohort 1, and the dark outer wing areas also more extensive in a number of specimens. These associated changes in pattern may represent a shift in the allocation of metabolic resources from ground colour pigmentation to melanization of the extended pattern elements, and it is notable that among the f. *helice* females which lack the orange background pigmentation, those from cohort 2 exhibited further developed pattern elements. Such pattern modification further suggests that cohort 2 developed under an unfamiliar temperature and daylength regime, since development can be expected to have only had an opportunity to have become canalized so as to produce 'normal' type and 'normal' f. *helice* phenotypes under conditions typically experienced in the wild.

Nylin & Svärd (1991) argue that in migratory species, local evolution will be prevented by recurrent gene flow and the need for genotypes each suited to a wide range of conditions, so that specimens from disparate latitudes should show little difference in size despite their developing under different temperatures and daylengths, as they report for *Pieris brassicae* L. (Lepidoptera: Pieridae). However, the capacity for organisms to exhibit different morphologies and life histories under different environmental conditions depends not on genetic differentiation, but on developmental plasticity, which the foregoing results show C. croceus to exhibit, and which has long been known in several other migratory species (e.g., Kettlewell, 1944, 1963). In fact, it is also upon developmental plasticity that the capacity for individuals of different genotype to exhibit different characteristics depends, for populations exhibiting identical morphologies can differ considerably in their genetic constitution (Oliver, 1977). Of course, evolutionary processes can then result in an increase in the importance of heredity in the extent to which the particular phenotypes are determined by heredity and by the environment (Waddington, 1961), and it is important to recognize that the hereditary factors that condition the phenotype an organism expresses under a particular environment can include not only genetic but also cytoplasmic factors (Ho, 1984). Moreover, the evolutionary processes involved need not require genetic variability or selection (Sonneborn, 1970; Cullis, 1983; Ho et al., 1983; Winokur, 1989), considerations commonly discounted or misunderstood in ecological studies.

Control of voltinism and phenotype in *Colias* butterflies appears to have been little studied (Friedrich, 1986). Rearing *ex ovo* under laboratory temperature and photoperiod regimes would improve understanding of the influence of environmental factors on growth rate, diapause induction and adult morphology. 'Transplant experiments' comparing samples of different origin under a suite of regimes would help determine

the relative importance of heredity and environment in conditioning their performance, when reciprocal crosses could specifically identify maternal (cytoplasmic) influences. Continued breeding programmes in conjunction with environmental manipulations could reveal novel hereditary and evolutionary phenomena (Winokur, 1989). No such studies involving a migratory butterfly are known to the author. Field and museum studies including specimens from northerly locations (Thomson, 1980; Eveleigh, 1984) on the other hand, would enable further characterization of latitudinal size trends.

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## References

- Cullis, C. A. 1983. Environmentally induced DNA changes in plants. CRC Crit. Rev. Plant Sci. 1: 117-131.
- Eveleigh, B. J. 1984. Clouded yellows overwinter. Bull. Amat. Ent. Soc. 43: 162.
- Ford, E. B. 1945. Butterflies. London: Collins.
- Friedrich, E. 1986. Breeding butterflies and moths—a practical handbook for British and European species. Colchester Books.
- Gardiner, B. O. C. 1984. The 1983 clouded yellow invasion. Bull. Amat. Ent. Soc. 43: 63-75.
- Ho, M.-W., Tucker, C., Keeley, D. & Saunders, P. T. 1983. Effects of successive generations of ether treatment on penetrance and expression of the *bithorax* phenocopy in *Drosophila melanogaster*. J. Exp. Zool. 225: 357–368.
- Ho, M.-W. 1984. Environment and heredity in development and evolution. In *Beyond neo-Darwinism*: an introduction to the new evolutionary paradigm (Ho, M.-W. and Saunders, P. T. eds.), pp. 267–314. London: Academic Press.
- Kettlewell, H. B. D. 1944. Temperature experiments on the pupae of (1) *Heliothis peltigera*, Schiff., and (2) *Panaxia dominula*, Linn. *Proc. S. Lond. Ent. Nat. Hist. Soc.* 1943-44A: 69-79.
- Kettlewell, H. B. D. 1963. The genetical and environmental factors which affect colour and pattern in Lepidoptera, with special reference to migratory species. *Entomologist* 96: 127–130.
- Nylin, S. & Svärd, L. 1991. Latitudinal patterns in the size of European butterflies. *Holarctic. Ecol.* 14: 192–202.
- Oliver, G. C. 1977. Genetic incompatibility between populations of the Nymphalid butterfly *Boloria selene* from England and the United States. *Heredity* **39**: 279–285.
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol* **106**: 85–108.
- Sonneborn, T. M. 1970. Gene action in development. Proc. R. Soc. (London) B. 176: 347-366.

Thomson, G. 1980. The butterflies of Scotland-a natural history. London: Croom Helm Ltd.

- Thomas, J. & Lewington, R. 1991. The butterflies of Britain and Ireland. London: Dorling Kindersley Ltd.
- Waddington, C. H. 1961. Genetic assimilation. Adv. Genet. 10: 257-294.
- Winokur, L. 1989. Developmental and evolutionary implications of cold shock effects in the speckled wood butterfly. PhD thesis, Southampton University.